

Intraspecific Interaction and Mechanisms of Population Regulation in Experimentally Limited Habitat

J. S. BANCROFT¹

Beneficial Insect Introductions Research Laboratory, USDA-ARS, 501. S. Chapel Road Newark, DE 19713-3814

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ABSTRACT Many populations of organisms deplete their resources, causing population growth rates to decline as population density increases. I used the sawtoothed grain beetle, *Oryzaephilus surinamensis* (L.), as a model to gain insight into the mechanisms of population regulation. Eight experiments differentiated the effects of crowding and food depletion on dispersal, mortality, and reproduction. Generally, food depletion caused increased mortality of immature beetles, sharply reduced oviposition, and increased adult dispersal. Rates of birth and death were both negative exponential functions of increasing density. The experiments quantify the trade-off between food and area in population regulation. These trade-offs varied with initial abundance of larvae and adults and show the risk of ignoring abundances of any life stages when characterizing vital rates. I contrast population regulation of *O. surinamensis* with *Tribolium* sp., and suggest *O. surinamensis* is a good alternative for experiments on population dynamics because of better mobility and shorter development time.

KEY WORDS *Oryzaephilus surinamensis*, Coleoptera: Silvanidae, population regulation, density dependence, habitat deterioration

A TREMENDOUS AMOUNT of effort has been spent trying to determine the forces that regulate populations, and the importance of density dependence continues to be vigorously debated (Wangersky and Cunningham 1957; King and Dawson 1972; Hassell 1975; Hassell et al. 1976; Dempster 1983; Dempster and Pollard 1986; Den Boer 1988; Hanski 1990, 1993; Turchin 1990; Krebs 1991, 1995; Woiwood and Hanski 1992; Turchin et al. 1998). These studies show that the predominant regulating forces on a population will vary over space and time. At the landscape level, geographic features or climatic conditions will limit populations. However, at the level of an individual's foraging area, high abundance causes negative behavioral interactions, which limits population density. By understanding the interactions that control density, we can estimate population densities and perhaps alter local conditions to manipulate the density of an organism of interest. To regulate a population, density-dependent feedback need only affect mortality or reproduction (Krebs 1978). A population's average abundance may be reduced by an increase in mortality rate or a decrease in reproductive rate. In general, the sum in these rates at any given density indicates the strength of the force that will drive population change. The underlying forces that cause density dependence are difficult to measure in the field, but laboratory studies have shown which forces may be important and used to guide field studies (Krebs 1995, Costantino and Desharnais 1996). This study used *Oryzaephilus surina-*

menis (L.) as a model to study the interactions that limit populations. I subjected *O. surinamensis* to eight laboratory experiments that quantified the response of adult and immature stages to variations in both density and amount of food.

Oryzaephilus surinamensis is generally encountered in stored grain, which has prompted studies of its reproduction and mortality at various temperatures, humidities, and in various grains (Back 1926; Thomas 1940; Howe 1956; Prus 1966; Curtis 1974; Arbogast 1976; Ciesielska 1994; Beckett et al. 1994; Collins et al. 1989; Jacob and Fleming 1989, 1990; Beckett and Evans 1994). In optimal conditions, females lay as many as 100 eggs over 1 yr and development lasts ≈ 3 , 13, and 5 d for the egg, larval, and pupal stages, respectively. Typically, *O. surinamensis* larvae pass through four instars. Studies suggests that *O. surinamensis* populations may be regulated by cannibalism on inactive stages (Beckett and Evans 1989, Jacob and Fleming 1989). *O. surinamensis* exploits temporary resources, and emigration can profoundly affect importance of cannibalism on eggs or pupae for the maintenance of declining resources (Hagstrum and Gilbert 1976, van Baalen and Sabelis 1995).

Direct interaction of conspecifics may stabilize a population while indirect interaction (mediated though resources) may cause oscillatory or even chaotic dynamics (May 1975). In the first two experiments, I measured rates of birth and death in response to crowding among beetles of different developmental stages. The direct intraspecific interaction that results from crowding is known to have profound effects on

¹ E-mail: jsbancr@udel.edu

population dynamics in a diverse set of organisms (Mertz and Robertson 1970, LeCren 1973, Mackie et al. 1978). Experiments three through five discriminated between the regulatory effects of competition for food and interference among conspecifics. The importance of direct and indirect interaction is an ongoing, fundamental ecological debate (Wangersky and Cunningham 1957, Arditi and Ginsburg 1989, Turchin 1990). In natural systems, reproductive individuals are known to affect immature development (Yoda et al. 1963, Hassell 1975, Hassell et al. 1976, Clutton-Brock et al. 1987) and immature mortality is often mediated through the indirect effect of immature resource competition (Yoda et al. 1963, Mertz and Robertson 1970, Klok and De Roos 1998).

Experiments six through eight used more natural mixed-stage populations to examine the joint effects of density and resource decline on rates of dispersal, mortality, and reproduction. These vital rates are affected by overexploitation of resources in numerous species (Yoda et al. 1963, Hassell et al. 1976, Newman 1989, Ostfeld and Canha 1995, Dolman and Sutherland 1997), but have not been studied together to quantify their relative importance. In experiment 6, I used patches with one amount of food and three initial stage distributions. By monitoring the population decline, I tested the relative effects of stages on patch dynamics. Understanding population response to resource availability is important for the management of threatened species and pest outbreaks (Caughley 1994, Dolman and Sutherland 1997). Individuals born into deteriorating habitat patches can extend survival by foregoing nonessential activities, but population persistence is contingent upon colonization of new resource patches (Ziegler 1978, Ciesielska 1994, Turchin 1986, 1989, Hastings 1992, Li and Margolies 1993, Matter 1996). In experiment 7, I monitored dispersal in response to the depletion of food resources. The final experiment was similar to experiment 7, but I quantified the rates of mortality and reproduction and removed immature beetles to better control food depletion. This multifaceted study with *O. surinamensis* elucidates dynamics of vital rates in response to changes in population density and food depletion. Armed with a detailed understanding of this system, one may (1) build a better pest management system for *O. surinamensis*, (2) focus field studies of other species to understand interactions most likely to be important, and (3) manage habitat to affect the desired change in population density.

Materials and Methods

All experiments were performed in an environmental chamber kept at $33 \pm 1^\circ\text{C}$ and $65 \pm 10\%$ RH. The beetle stock was acquired from the U.S. Grain Marketing Research Laboratory in Manhattan, KS, in 1995. Beetle stock was maintained on a diet of 95% wheat flour and 5% brewers' yeast by weight. Standard film vials (3 by 5 cm) with ventilating pinholes were used as patches. I measured dispersal with an apparatus adapted from Prus (1963, 1966). Latex tubing con-

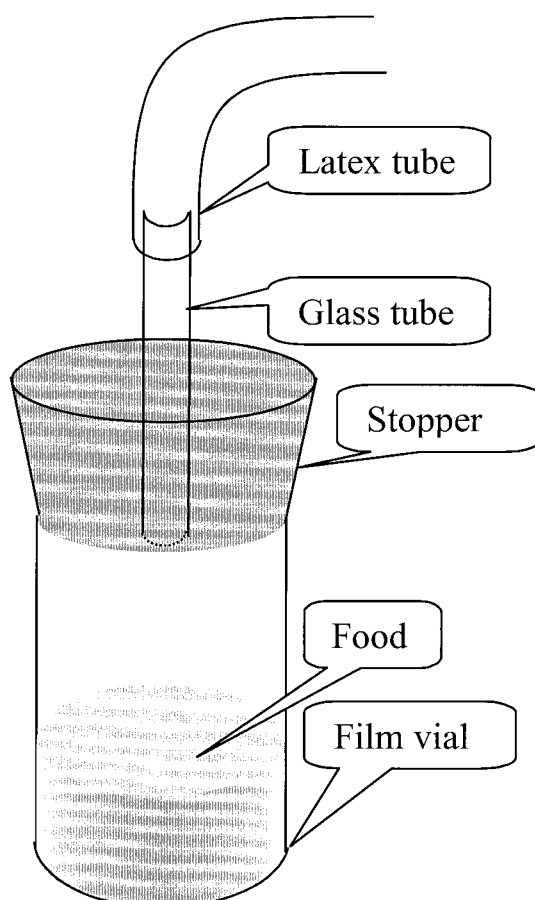


Fig. 1. Apparatus used to measure dispersal. Latex tube of 10 cm leads to empty vial with fluon coated inner walls, which trap dispersing beetles.

nected vials and allowed beetles to disperse, but Fluon prevented backward dispersal to the source vial (Fig. 1).

Experiment 1: Effects of Adult Presence on Immature Cohorts. In this experiment, I tested the effect of the presence of adults on larval development time and survival. I placed 20 adults from the stock culture in a vial with 8.0 g of food for 1 wk. This procedure was performed in 42 vials. The adults were then removed, leaving eggs and larvae. I did this because handling eggs causes mortality, and I wanted to let adult females oviposit naturally. Six treatment groups of seven vials each were established. I used four treatments to measure the effect of adult presence during one of the succeeding 4 wk. Each week, 10 adults were added to a set of vials for that treatment week and removed from the set of vials from the previous treatment week. Two groups were controls. One was sifted each week to mimic the disturbance associated with removing adults, and the other was left undisturbed. I recorded the number of emerging adults daily. An analysis of variance (ANOVA) was performed to test whether the presence of adults in any week affected either

number of emerging adults or development time (StatSoft 1999). Contrast tests were then performed between the controls and the individual weeks to identify significant effects.

Experiment 2: Effects of Density in Immature Cohorts. In this experiment, I measured the effect of immature density on development time and survival. To obtain cohorts of equal age, colony adults were placed in new diet for 24 h, and, after 3 d, equal-age first instar larvae were placed in vials with 0.25 g of food. Treatments of 2, 5, 10, 20, 40, and 80 larvae were replicated 17, 13, 10, 6, 6, and five times each, respectively. I noted emerging adults daily until all living beetles had emerged.

In this and subsequent experiments, I regressed the proportion of surviving individuals on the number of individuals starting in each replicate. The use of proportions caused unequal variances across different levels (densities) because of the limited number of response values possible. For example, a replicate with two individuals must have a survival rate of 0.0, 0.5, or 1.0. Therefore, I weighted the resulting proportion of survivors for each replicate in the regression to stabilize variance (Steele and Torrie 1980). This caused replicates with more individuals to be more important in the regression while maintaining the original degrees of freedom of the experiment.

Experiment 3: Effects of Amount of Food on Immature Cohorts. This experiment was used to quantify the effect of varying the amount of food on immature development rate and survival. Cohorts of 10 first instars were placed on 0.05, 0.10, 0.15, 0.20, and 0.25 g of food. Six replicates for each treatment were performed. Because survival varied among replicates, the emergence times were weighted by the number of beetles that successfully pupated in each replicate. I weighted the resulting proportion of survivors as described in the methods of experiment 2. used linear regression to analyze the data.

Experiment 4: Effects of Food Quality on Larvae and Adults. In this experiment, I considered the cumulative effects of feeding and defecation on reproduction and survival. I initiated vials with 0.5 g of food and either adults, larvae, or adults and larvae. Each treatment had nine replicates. To measure the effect of food quality on larval development, 20 first instar larvae were left in vials for 14 d. Beetles were sifted and the numbers of larvae, pupae, and adults were noted. Food was reused with 20 more first instars three more times. The results were used to test the effect of cumulative food deterioration on development time and survival. To measure the effect of food quality on adults, 10 adults were placed in a vial for 7 d. I counted the eggs, larvae, surviving adults, calculated reproduction, and survival. The food was then reused with 10 more adults four more times. Finally, 10 adults and 20 larvae were placed in vials to compare with single-stage treatments. I censused all stages every week, replaced adults every week and larvae every 2 wk. When the 20 larvae had fed for 1 wk, on alternate weeks, they were placed back in the depleted food for a second week. The results were analyzed using gen-

Table 1. Design of food conditioning experiment with treatment replicates

Adult density (adults per week)	Conditioning (adults per week)				
	0	1	10	20	40
1	21	17	4	8	3
10	14	4	6	5	3
20	8	4	4	3	4
40	13	3	4	4	3

eral linear model (GLM) to compare larval development time, larval survival, adult reproduction, and adult survival across treatments (SAS Institute 1998, StatSoft 1999). Adult oviposition and mortality were analyzed by comparing the adults-only treatment to that with adults and larvae. Larval survival and development were analyzed by comparing the larvae-only treatment and the corresponding second week census of the adults and larvae treatment.

Experiment 5: Effect of Food Quality and Density on Adults. This experiment was designed to measure the effects of both food deterioration and adult density on reproduction and survival. Vials with 0.05 g of food were either not conditioned or conditioned by 1, 10, 20, or 40 adults. After 1 wk, I sieved all beetles from the food. The conditioned food was then reused with 1, 10, 20, or 40 adults. After 1 wk, the live eggs, larvae, and adults were recorded. Table 1 lists the number of replicates for each treatment level. Multiple regression was used to test the effect of cumulative feeding time and treatment density on both per capita reproduction and per capita survival. I weighted the resulting proportion of survivors as described in the methods for experiment 2.

Experiment 6: Effects of Initial Stage Distribution on Population Decline. The natural progression of population decline was observed over time to measure the effects of cumulative feeding time on mortality and reproduction. There were three treatments that began with initial beetle abundances of either 10 adults, 20 larvae, or both 10 adults and 20 larvae. I initiated four vials with 0.25 g of food for each treatment. The abundance of larvae, pupae, adults, and dead adults was censused every 2 wk and live stages were put back in the vial with depleted food. I continued to census populations until all beetles were dead. The first test was an ANOVA comparing the extinction times, when the last beetle died, among the three treatments. The densities of active stages were then used in a repeated measure ANOVA that compared the three initial treatments with respect to both mortality and reproduction. The comparison of initial stage distributions provides a more natural demonstration of the process of depletion and eventual extirpation in *O. surinamensis* populations. In the treatment with both adults and larvae, the survival time for each replicate was scaled to a maximum of one. I then used least squares regression to fit the survival data with a logistic equation and compare the relative survival of the stages.

Experiment 7: Effect of Density on Dispersal. I set up a total of 80 dispersal trials in the apparatus de-

scribed in the general methods above (Fig. 1). Source vials with 40 adults and 0.25 g food were initiated in eight replicates. The receiving vials were checked for immigrants every few days. When an individual was found in the receiving vial, it was scored as having arrived in the middle of any missed days and was placed back in the source vial to control beetle density. Because dispersal events were highly infrequent, it is improbable that any single *O. surinamensis* individual was counted more than once. For each replicate, dispersal monitoring continued until all beetles were dead due to starvation. Because of low dispersal rate in the first set of trials, 72 more replicates were added. With 0.05 g of food in the source vials, 46 replicates were initiated with 40 adults each. I also initiated 26 replicates and 100 adults with 1.0 g in the source vials.

Per capita dispersal per replicate was subjected to ANOVA for the effect of beetle abundance and amount of food. I also scaled the logistic survival function from experiment 6 to the maximum observed survival time. This provided the estimate of adult survival over time. Next, the daily per capita dispersal probability was calculated for each day of each replicate by dividing by the estimated number of surviving adults. The estimated survival allowed the calculation of cumulative feeding in adult-days. For each replicate, the cumulative feeding time was scaled to 1 by dividing by the total cumulative feeding that had occurred when the last beetle died. These scaled variables were used to explore the relationships between dispersal frequency and both the proportion of surviving adults and the cumulative feeding time.

Experiment 8: Effects of Deteriorating Food on Dispersal, Mortality, and Reproduction. In this experiment, I determined rates of dispersal, mortality, and reproduction in response to deteriorating habitat. In each of 13 vials, I placed 0.25 g of food and 20 adult *O. surinamensis*. The dispersal apparatus was used to capture dispersing beetles. I censused populations at 2-wk intervals until all beetles in all replicates had died. In contrast to experiments 6 through 8, I removed immature beetles to better control cumulative feeding time. I censused eggs, larvae, pupae, adults, and dead adults to assess per capita rates of reproduction, dispersal, and mortality. Per capita rates of survival and mortality were used to fit nonlinear functions with respect to both survival time and cumulative feeding time.

Results

Experiment 1: Effects of Adult Presence on Immature Cohorts. The presence of adults during larval development significantly increased average development time (Fig. 2A). Using Tukey's multiple contrast tests (StatSoft 1999), beetles exposed to adults in weeks 1, 2, and 3 had significantly longer development times than the sieved control ($F = 7.0$; $df = 5, 35$; $P < 0.01$). The effect was strongest when the immatures were small and vulnerable to adult cannibalism. The rate of survival and development in the unsieved con-

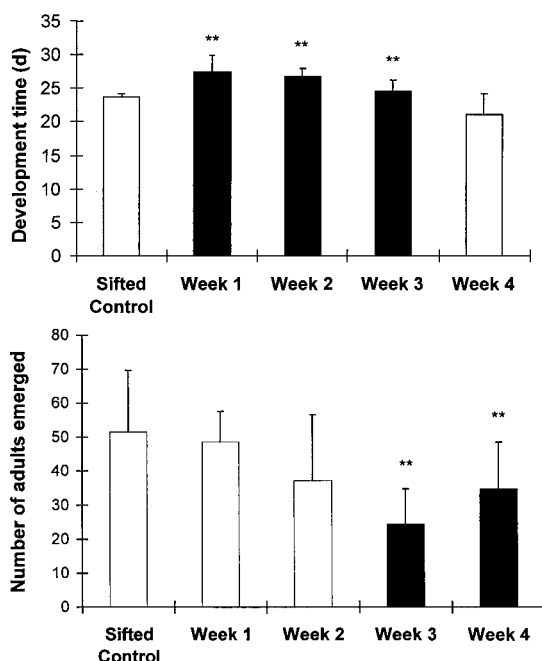


Fig. 2. Effect of adult presence on (A) development time and (B) immature survivorship. The week that adults were present during immature development is shown on the x-axis. Whiskers indicate standard error. **, Shaded bars are significantly different than the control ($P < 0.01$).

trol was not significantly different from the sifted control (data not shown). Survival rates of immatures followed a different pattern than development time (Fig. 2B). Significantly fewer larvae survived when adults were present during weeks 3 and 4 than in weeks 1 and 2 ($F = 4.4$; $df = 5, 35$; $P < 0.01$).

Experiment 2: Effects of Density in Immature Cohorts. Before re-weighting, survival proportions were arcsine-square root transformed to normalize distributions (StatSoft 1999). The proportion of larvae that successfully completed development decreased significantly with increasing cohort density ($F = 6.5$; $df = 1, 55$; $P < 0.01$). The development time for larvae increased significantly with increasing cohort density ($F = 231.3$; $df = 1, 55$; $P < 0.01$). Although larval survival declined 32% over the density levels, adult emergence was only delayed 5% for large cohorts (Fig. 3).

Experiment 3: Effects of Amount of Food on Immature Cohorts. Regression analysis on arcsine-square root transformed data indicated that larger amounts of food caused significant increases in the proportion of surviving larvae ($F = 13.8$; $df = 1, 30$; $P < 0.01$; Fig. 4A). Greater amounts of diet significantly decreased per capita development time ($F = 36.4$; $df = 1, 30$; $P < 0.01$; Fig. 4B). Tukey's honest significant difference (HSD) test (StatSoft 1999) suggested that only the 0.25 g treatment was significantly different from the other treatments ($F = 53.9$; $df = 4, 27$; $P < 0.01$).

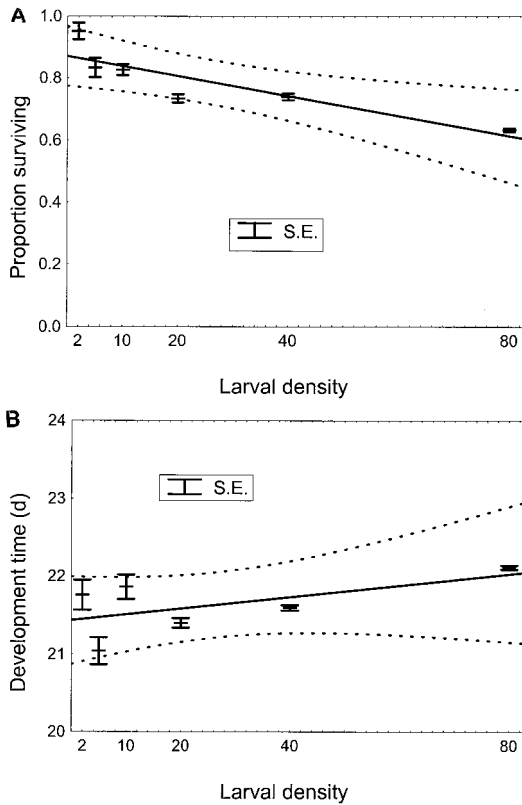


Fig. 3. Effect of crowding on (A) proportion of larval surviving, $y = 0.834 - 0.027x$ ($R^2 = 0.26$) and (B) development time to adult emergence, $y = 21.38 + 0.0086x$ ($R^2 = 0.19$). Whiskers indicate standard error. Dashed lines are 95% CI.

0.01). This was the largest amount used and suggests that 0.025 g of diet is sufficient to develop and suppress cannibalistic behaviors.

Experiment 4: Effects of Food Quality on Larvae and Adults. The proportion of surviving larvae was significantly higher for the treatment with larvae than with adults and larvae ($F = 19.9$; $df = 1, 56$; $P < 0.01$; Fig. 5A). The increasing survival trend was unexpected; this contradicted my expectation that cannibalism should increase as food quality declines. The proportion of surviving larvae that pupated was significantly different between the larvae and adults with larvae treatments ($F = 11.7$; $df = 1, 56$; $P < 0.01$).

The effects of the presence of larvae on adult reproduction and mortality are shown by comparing the replicates of adults alone with those having adults and larvae. Adult reproduction was not significantly affected by the presence of larvae ($F = 0.5$; $df = 1, 80$; $P = 0.76$). Reproduction decreased over time ($F = 70.0$; $df = 1, 80$; $P < 0.01$) and indicated that degraded food decreases oviposition rate or increased cannibalism (Fig. 5B). Mortality was not significantly different between the adults alone and the adults-with-larvae treatment ($F = 0.22$; $df = 1, 80$; $P = 0.64$). Larvae appeared to have little effect on adult reproduction or mortality.

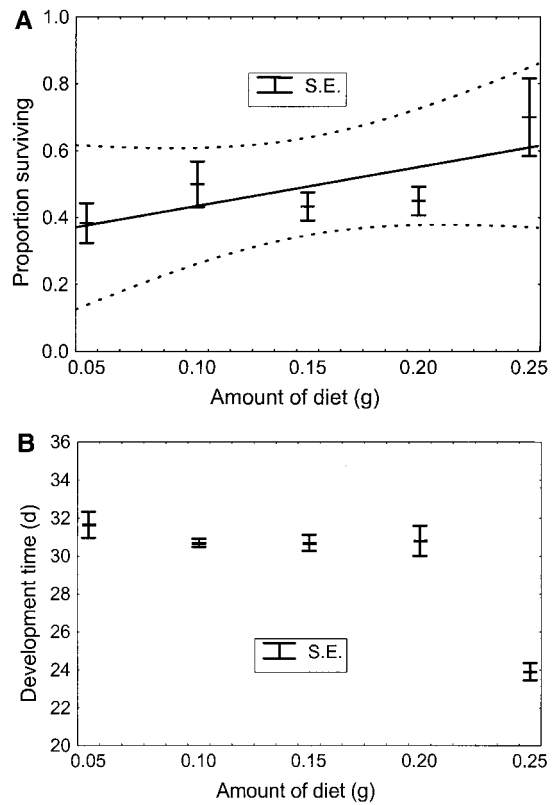


Fig. 4. Effect of amount of diet on (A) larval survival, $y = 1.49x + 0.29$ ($R^2 = 0.29$) and (B) development time to adult emergence, $y = -41.4x + 35.2$ ($R^2 = 0.53$). Whiskers indicate standard error. Dashed lines are 95% CI.

Experiment 5: Effect of Food Quality and Density on Adults. Rates of per capita reproduction were transformed $\ln(x + 1)$ to normalize distributions. Both greater density and greater cumulative feeding caused significant decreases in egg abundance per adult ($F = 5.3$; $df = 1, 142$; $P = 0.02$ and $F = 17.7$, $P < 0.01$, respectively). The Akaike information criterion was used to select the exponential functions over a planar surface in their fit of the reproductive rate (AIC = 57, $R^2 = 0.62$ versus AIC = 123, $R^2 = 0.57$, respectively; Fig. 6A). Both greater density and cumulative feeding caused significant increases in the proportion of dead adults ($df = 1, 142$, $F = 79.1$, $P < 0.01$ and $F = 38.7$, $P < 0.01$, respectively). Again, exponential functions fit the mortality rate better than a planar surface (AIC = -124, $R^2 = 0.568$ versus AIC = -109, $R^2 = 0.527$, respectively; Fig. 6B).

Experiment 6: Effects of Initial Stage Distribution on Population Decline. An ANOVA for extinction time showed significant differences among treatments with adults, larvae, and adults-with-larvae (Table 2), and the mean survival times for the treatments were 21.4, 14.4, and 12.0 wk, respectively. The pair-wise comparison of treatments suggests that larval presence dramatically decreased time to extinction. How the initial presence of adults or larvae affected time to

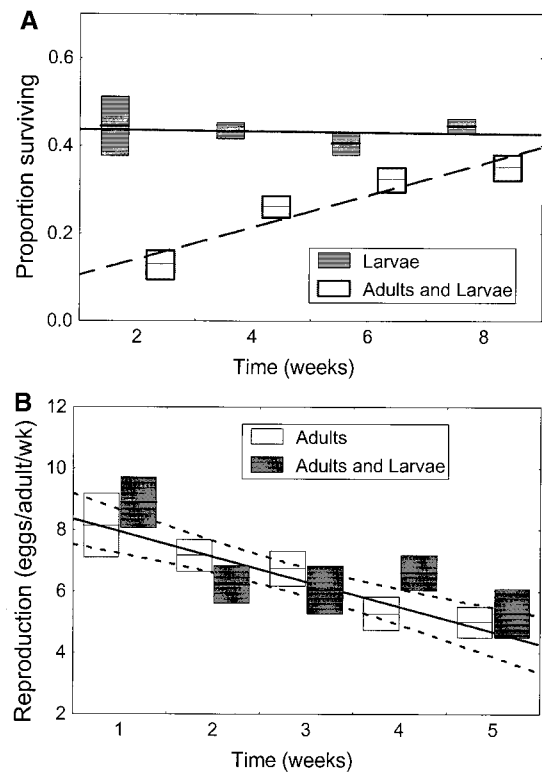


Fig. 5. Effect of cumulative feeding time on (A) proportion larvae surviving, (B) reproduction, $y = 8.79 - 0.75x$ ($R^2 = 0.21$).

extinction was explored in patterns of survival and reproduction.

To compare the effects of initial stage abundances on reproduction and survival, a number of steps were performed before ANOVA. To normalize distributions, per capita mortality rate was square-square root transformed, and per capita reproductive rate was log transformed. The ANOVA showed that the initial stage abundance affected mortality and reproduction (Table 2) with pair-wise comparisons. The rate of adult mortality was much higher in the larval treatment (31 versus 23%/wk). Apparently, the larvae exhausted food supplies, and adults could not replace this loss by scavenging or cannibalizing on larvae. In a similar comparison, the rate of reproduction was much higher in the larval treatment (2.8 versus 1.5 eggs/adult/wk). In this case, a flush of new adults emerged to exploit while the food quality was still high. Finally, a greater number of pupae were observed in the treatment with adults, versus the adults and larvae treatment (13 versus 2%/larva/wk, Fig. 7A). This shows the overexploitation of food by larvae and subsequent cannibalism on pupae. In the treatment with both adults and larvae, I scaled survival time for each replicate and then fitted survival data with a logistic equation (Fig. 7B). Larvae were eliminated more quickly from deteriorating food than adults. This may be due to differential ability between the stages

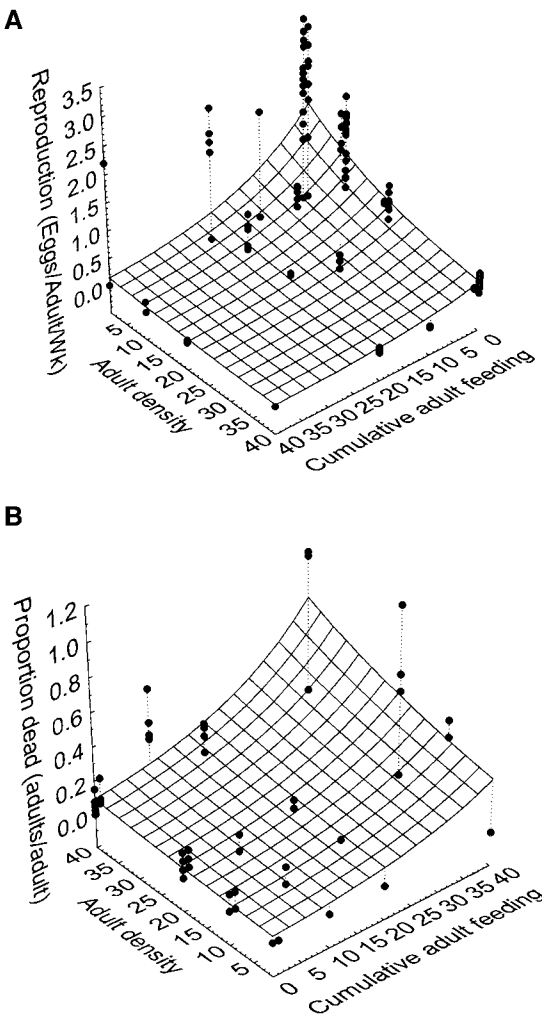


Fig. 6. Effects of cumulative feeding time and adult density on (A) reproduction = $\exp(0.59 + 0.061\text{feeding} + 0.038\text{density})$ ($R^2 = 0.62$), and (B) proportion dead = $\exp(-3.25 - 0.052\text{feeding} + 0.022\text{density})$ ($R^2 = 0.57$).

to use poor quality food or direct interference or cannibalism.

Experiment 7: Effect of Density on Dispersal. The daily overall rate of adult dispersal was 3.23×10^{-5} per day. The ANOVA results did not show that the number of dispersing beetles varied with density of adult per gram of food ($F = 1.3$; $df = 12, 67$; $P = 0.21$). I then

Table 2. AOV results and probability values of planned comparisons for treatment pairs using LSD

Response variable	F	df	P value	Treatment pair		
				1 v. 2	1 v. 3	2 v. 3
Extinction time	8	2, 9	0.01	0.02	<0.01	0.34
Reproduction	15	2, 18	<0.01	0.03	<0.01	<0.01
Mortality	165	2, 18	<0.01	<0.01	<0.01	0.23

Treatment codes: 1 = 10 adults, 2 = 10 adults with 20 larvae, 3 = 20 larvae.

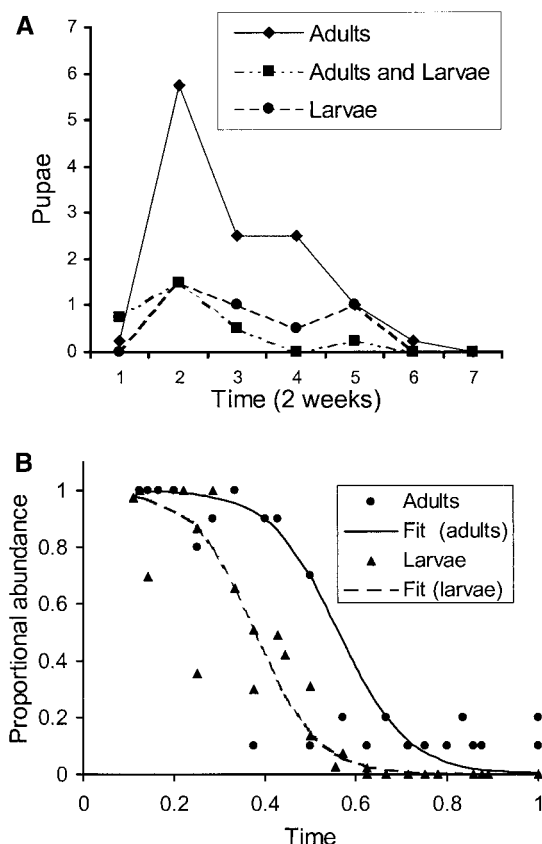


Fig. 7. (A) Mean abundance of pupae through time in for each treatment. (B) Effect of time on abundances of stages in mixed populations. The maximum abundance of a stage and time to extinction for each replicate were used to scale relative abundance and duration, respectively. Larvae = $1 - (\exp((x - 0.378)/0.068) / (1 + \exp((x - 0.378)/0.068)))$ ($R^2 = 0.78$). Adults = $1 - (\exp((x - 0.563)/0.075) / (1 + \exp((x - 0.563)/0.075)))$ ($R^2 = 0.67$).

scaled the survival time to a maximum of one for each replicate, and created a histogram of the 236 dispersal events over time (Fig. 8A). The increase in dispersal frequency toward the middle of the experiment corresponds to induced dispersal of adults when food became depleted. The reduction in dispersal frequency corresponds to the subsequent starvation of adults. I found the large amount of dispersal suspicious in some replicates and plotted a histogram of total dispersal events per replicate (Fig. 8B). The negative binomial distribution should fit these rare events if beetles disperse independently, but a Kolmogorov-Smirnov test indicates that dispersal diverges from this distribution ($d = 0.42$, $P < 0.01$).

To examine dispersal over time, I fit nonlinear relationships between dispersal frequency and the proportion of both adults that died over time and cumulative feeding over time. Dispersal frequency of adult *O. surinamensis* decayed exponentially as the proportion of dead adults increased (Fig. 8C). An-

other likely cause of dispersal was that the frequency of dispersal increased exponentially as cumulative feeding time increased (Fig. 8D).

Experiment 8: Effects of Deteriorating Food on Dispersal, Mortality, and Reproduction. The average stage distribution showed that adults predominate as food deteriorates (Fig. 9A). I calculated per capita rates of adult mortality and reproduction for each replicate. A logistic distribution fitted the mortality rate while reproduction declined exponentially over the course of the experiment (Fig. 9B). These curves help explain Fig. 9A. Over time, reproduction declined quickly as food quality declined. When conditions became extremely poor adults interfered and scavenged other stages before they eventually starved. I next calculated cumulative food consumption to examine its affect on reproduction, mortality and dispersal. The cumulative feeding was calculated from the periodic census of beetles in each replicate. I scaled the cumulative feeding of each trial to a maximum of one and plotted the adult per capita reproduction, mortality and dispersal (Fig. 9 C-E). Strong nonlinear responses were evident. Only 10 dispersal events were observed; however, the graph suggests that the dispersal events were induced as cumulative feeding exhausted food supplies.

Discussion

Oryzaephilus surinamensis has strong negative exponential feedback on reproduction, mortality and dispersal in response to density and food quality. The experiments were designed to measure the intraspecific controlling mechanisms of *O. surinamensis* populations. Adult beetles demonstrated negative feedback regulation by causing increased development time and rate of cannibalism on immature beetles. Similarly, immatures interfered with the development and successful pupation of cohort-mates. To a larger degree, food depletion increased immature mortality and development time. Finally, adult dispersal is induced as food quality becomes depleted. By quantifying the interaction within and among stages of *O. surinamensis*, I characterized an empirical model system that is useful for studying complex population dynamics. The rapid development and easy manipulation of all stages in laboratory experiments makes *O. surinamensis* a fine alternative to *Tribolium* or *Drosophila*. Models that use nonlinear functions to represent vital rates in response to habitat conditions exhibit complexity in population dynamics (Hassell et al. 1976, Hastings 1992). Nonlinear rates of birth and death in response to conspecific density have been difficult to demonstrate in natural populations (Dennis et al. 1995) but empirical models have shown great utility for demonstrating complex population dynamics (Park 1946, Huffaker 1958, King and Dawson 1972, Dennis et al. 1995, Costantino and Desharnais 1997).

The first three experiments show that pupal cannibalism by active stages exerts a strong regulatory force on beetle abundance. In experiment 1, the effect of adult presence on immature development and survival

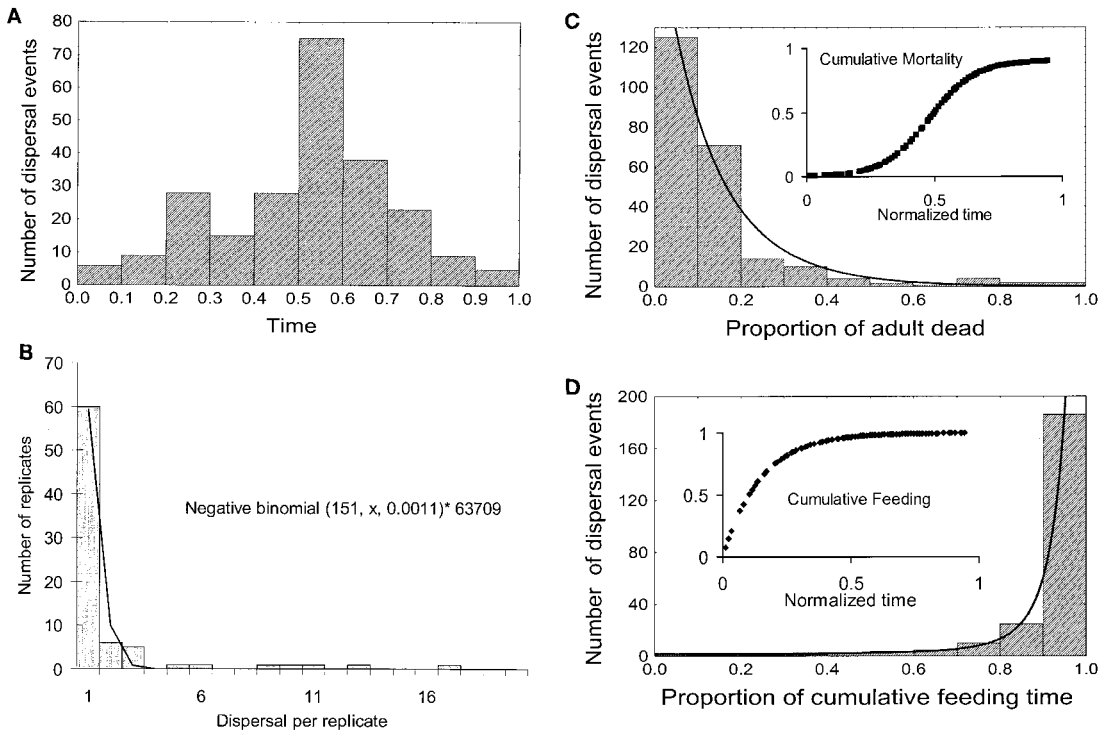


Fig. 8. (A) Histogram of dispersal events over proportional survival time. (B) Histogram of replicates over the number of dispersal events per replicate. Curve fit is negative binomial distribution. Histograms of dispersal events by (C) estimated proportion of density, $y = 5 \times 10^{-6} \exp(17.5 \exp(-0.49x))$, and (D) estimated proportion of cumulative feeding, $y = 1.67 \exp(0.028 \exp(5.42x))$.

is strongest when pupation occurs. This result indicates that adults kill the relatively defenseless pupae. Because the pupal carcasses were intact, it appears that the adults were not consuming the pupae, but adults were reducing future competitors for the limited food resources. In the experiments with even-age cohorts, I believe there was enough food for development of all beetles and decreasing adult emergence with density was due to cannibalism. The consumer: food ratio was used to compare the effect of cohort density and amount of food on mortality. In experiments 2 and 3, the estimated rates of mortality were compared over the observed range of consumer: food ratio. Estimated rates of mortality were compared between a five-fold range of larval density in a constant amount food and a five-fold range of amount of food in a constant larval density. The mortality rate increased 30% with increasing cohort size and decreased 16% with amount of food. Therefore, the amount of food had twice the impact on mortality as size of cohorts. Adults readily move on the flour surface, and immature beetles may be more successful when fully concealed in flour. There are no safe refuges but burrowing larvae may conceal themselves for molting and pupating when in larger amounts of food. This threshold in immature mortality between 0.2 and 0.25 g can be explained by the effect of food abundance (Fig. 4B).

The consumer: food ratio and the ratio of adults to larvae are related to the theoretical debate over the best functional form to use in modeling the mortality rate (Hassel 1976, Arditi and Ginsberg 1989, Abrams 1994, Akcakaya et al. 1995). Whether the ratio of predator to prey is a useful mathematical term in the approximation of the mortality rate depends on the nature of the interaction. Sokoloff (1999) has argued that *Tribolium* populations are best represented as a predator-prey system. Like *Tribolium*, *O. surinamensis* mortality is influenced by complicated nonlinear relationships with availability of food and density dependent cannibalism. Because of the regulatory influence of nonlinear processes, researchers should be vigilant about checking the assumptions of what variables are involved in interactions.

Although cannibalism occurs, the results show strong competition for food between the life stages. Cannibalism on larvae may provide some benefit for adults, but the benefit was not evident when reproduction was measured in the presence of larvae (Fig. 5C). The residual food was weighed after this experiment (#4) to see if it was depleted at a rate proportional to the cumulative time of feeding. The total amount of food consumed by the adults and larvae separately was 33% greater than when together ($F = 42.0$; $df = 2, 24$; $P < 0.01$). The average weight of food consumed per larvae was 37% of that of adults. Be-

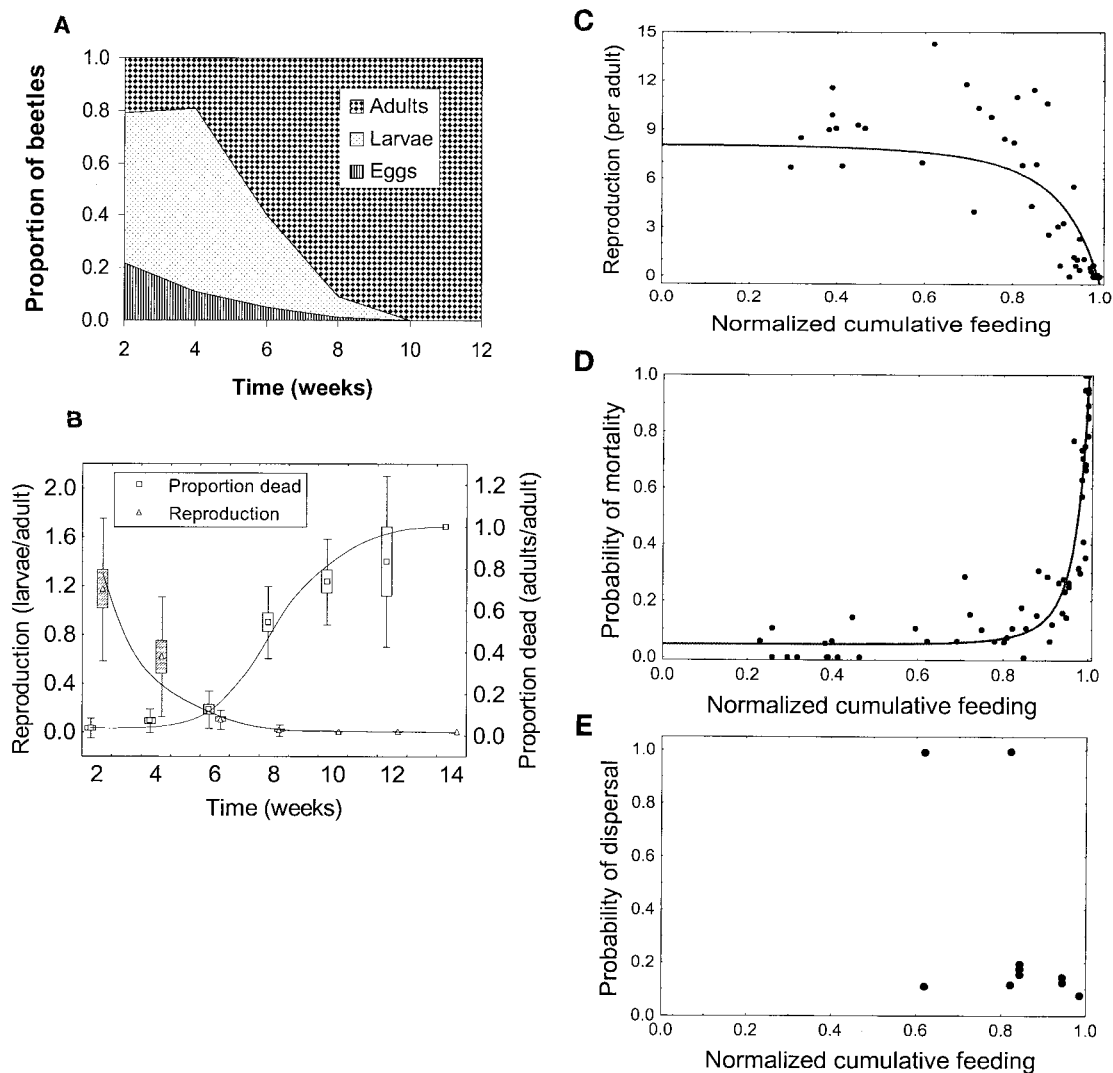


Fig. 9. Effect of time on (A) stage distribution and (B) mortality and reproduction. Effect of estimated cumulative feeding on probability of (C) reproduction, $y = 9.08 \cdot \exp(-0.03 \exp(4.34x))$ ($R^2 = 0.63$), and (D) mortality, $y = 0.04 \exp(10^{-4} \exp(10.3x))$ ($R^2 = 0.97$), and (E) dispersal.

cause larvae typically make up three fourths of populations, adults and larvae are approximately equal competitors for food in natural mixed-stage populations.

In experiment 4 with reuse of food, the trend toward greater larval survival when in the presence of adults was unexpected (Fig. 5A). Apparently, adults interfere with development and decrease rates of molting and pupation, which reduces exposure of the inactive stages to the threat from cannibalism by adults. Because the survival of larvae alone did not vary with time, 0.5 g of food is enough for 80 beetles to develop. In addition, the proportion of surviving larvae that pupated decreased precipitously over time (Fig. 5B). This threshold effect probably is the combined result of food becoming unsuitable for larvae to complete development and increased adult cannibalism on lar-

vae. Under conditions of limited resources, elimination of immatures is a common phenomenon in vertebrate species as well (LeCren 1973, Clutton-Brock 1997, Turchin and Hanski 1997). The common method of self-regulation by eliminating immatures makes *O. surinamensis* useful as a model system.

The dispersal reaction of *O. surinamensis* to poor food quality makes an interesting comparison with *Tribolium*. Prus (1966) suggests that *Tribolium* will disperse in response to larval presence, but none of my research suggests larvae influence adult *O. surinamensis* to disperse. In addition, comparing Poisson-distributed dispersal with observed dispersal suggests *O. surinamensis* may disperse in groups (Fig. 8C). Pierce et al. (1983) worked on the pheromone chemistry of *O. surinamensis* and found that males feeding on high-quality food will emit a pheromone that attracts other

beetles. Although my vials were without directed airflow, the directed movement of dispersing beetles may explain the observed distribution. Interestingly, Pierce et al. (1983) reported that at high concentrations the pheromone acts as a repellent. A major dispersal impetus in both *Tribolium* and *O. surinamensis* is poor food quality. For *Tribolium* dispersal, food quality seems to be more important than density (Naylor 1959, 1961, 1965). *O. surinamensis* dispersal accelerates rapidly with food depletion (Fig. 8D).

Stage-specific interaction within *O. surinamensis* provides an interesting comparison with *Tribolium* (Sokoloff 1974). Hastings and Costantino (1987) describe a model of *Tribolium* whose populations oscillate when egg cannibalism depends on the age of larvae. Their model's instability depends on periodic population fluctuation due to a large supply of eggs and the flush of synchronous larval pupation. Because *O. surinamensis* is less fecund than *Tribolium*, egg cannibalism by larvae may not be as important. If oviposition is strongly inhibited at high density in *O. surinamensis* then reproductive lifespan is likely to play an important role in determining patch abundance (Rich 1956, Logan and Allen 1992, Benoit et al. 1998, Longstaff 1998). The long reproductive lifespan of *O. surinamensis* may counteract the unstable dynamics of larval interaction. With long overlapping generations, *O. surinamensis* adult number is a stabilizing force on population fluctuations (Neubert and Caswell 2000). The differences in birth, death, and dispersal between *O. surinamensis* and *Tribolium* strengthen our understanding of the mechanisms that explain overall population dynamics (Rich 1956, Breton 1962, Young 1970, Desharnais 1996, Sutherland 1996, Benoit et al. 1998).

Studying only specific stages of an organism is a great risk because rates of reproduction or mortality may vary among life stages. This risk is illustrated by the effect of initial stage distribution on population decline (experiment 6). When populations were inoculated with adults alone, the survival time was much longer than when larvae were also introduced. If these were animals we wanted to protect, very few individuals would be left by the time we discovered a decline in adults. Healthy populations have many larvae, and we know that immature stages are eliminated by density dependent interactions.

These results provide a solid foundation for understanding *O. surinamensis* population dynamics, and show how beetle density and food limitation cause direct and indirect population control in *O. surinamensis*. I suggest that researchers studying organisms that deplete their food resources measure variation in immature development and mortality over periods of resource cycling. Conversely, variation in the interaction of life stages may indicate variation in a key resource hitherto unknown.

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